PEDAL EXPANSION IN THE NATICID SNAILS.
I. INTRODUCTION AND WEIGHING EXPERIMENTS [1]

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Possession of an enormously expanded foot, partially enclosing the shell, is characteristic of living naticid snails (or "moon-snails"), and is commonly employed as a diagnostic feature for the group. The adaptive significance of this apparently disproportionate pedal expansion is two-fold. First, the expanded wedge-shaped propodium and the metapodial folds covering the shell obviously contribute to the efficiency of "plowing" locomotion, as the moon-snail moves along on, and through, sandy substrata. Secondly, the naticids are predaceous carnivores with protrusible proboscides, and employ their extensible pedal lobes to manipulate and enfold their molluscan prey. Physiological aspects of this expansion are reported in the present paper, and in the succeeding one (Russell-Hunter and Apley, 1968), the existence of a pedal water-sinus system is demonstrated conclusively, and the functioning of the naticid water-sinus system is discussed.

In his recent, and otherwise excellent, review of locomotion in molluscs, Morton (1964) largely dismisses the possibility of water uptake being involved in naticid expansion, and notes that no modern workers (over the last eighty years) have claimed to demonstrate any aquiferous system of pedal canals. In the last volume of her fine, comprehensive survey of the invertebrates, Hyman (1967) similarly denies the occurrence of internal spaces for water in the naticid foot. Thus, there is clearly a need for an unequivocal demonstration of the use of a pedal water-sinus system in the expansion of naticids, and it is hoped that the present papers will provide it. However, a brief review of why Morton, Hyman, and others were misled by earlier published accounts, and reached their erroneous conclusions seems required.

HISTORICAL INTRODUCTION

In the early nineteenth century, a number of workers on the Mollusca believed that expansion of various structures in a wide variety of marine molluscs was due to the direct uptake of sea water into the blood spaces. Molluscan anatomists from the time of Cuvier onwards had clearly described the large number of protrusible or distensible structures: tentacles, proboscides, ctenidia, penes, and the mantle and foot themselves, which structures in typical molluscs contained only *retractor* musculature. Dilation with fluid to turgescence was early recognized as a characteristic method of protraction. Universal theories involving sea-water

uptake in the mechanisms of pedal dilation in all bivalves and snails were dismissed after a number of workers in the 1880's, but most notably Carrière (1882) and Ray Lankester (1884), had shown that, in many different species in both classes, dilation was achieved by the influx of blood withdrawn from other parts of the body. It remains true that the majority of molluscan organs are dilated by hydraulic mechanisms involving the blood within the spaces of the hemocoel. Carrière (1882) also gives a fairly extensive account of the earlier literature. At almost the same time Schiemenz (1884, 1887) claimed to have demonstrated a system of "aquiferous" tubes in the foot of a naticid snail. His observations were made on the relatively large form, *Polinices josephinus*, and they were undoubtedly accurate as regards both the anatomy and the functioning of the system. Schiemenz had earlier been, with Carrière and Ray Lankester, among the group of malacologists strongly opposed to the more general theories of sea-water uptake, but he chose to work on a representative of what now appears to be the *only* group of gastropods to have a water-sinus system—the family Naticidae. As might be expected, the generalization of hemal distension was widely accepted, and Schiemenz's exceptional case ignored or even denied (see, for example, such general surveys of the Mollusca as those of Lankester, 1883, 1891; Simroth, 1879, 1896–1907; and Pelseneer, 1906).

It should be remembered that earlier workers on the mechanics of movements in soft-bodied animals were sometimes confused as to the physiological capabilities of muscle. Simroth (1879), for example, even invoked "active extension" of muscles in discussing molluscan mechanics. The fact that muscles in *all* animals can exert force *only by contracting* had been established by the beginning of this century. The concept of antagonistic sets of muscles acting around a hydrostatic or hydraulic skeleton in soft-bodied animals became clarified, and an early classic account of the molluscan hemocoel as the "force-transmitting" skeleton acted upon by antagonistic muscles is that of Biederman (1905).

Later workers on snail pedal anatomy and mechanics (among them; Weber, 1924; Rotarides, 1934; Lissmann, 1945a, 1945b) emphasized the importance of the hemal hydraulic skeleton. Perhaps the first worker since Schiemenz to investigate problems of dilation in a naticid was Morris (1950) who, working on the smallish Australian species, *Uber strangei*, produced rather inconclusive evidence of water uptake, and claimed that partial expansion was possible in air. A group of unrelated gastropods where the foot undergoes turgid hypertrophy encompasses the South African species of *Bullia* (family Nassariidae), whose ecology closely parallels that of the naticid genus *Polinices*. Once thought to involve water uptake (Gilchrist, 1916), modern investigation of pedal expansion in *Bullia* (Brown and Turner, 1962; Brown, 1964), using such methods as radiography with the blood loaded with radio-opaque dyes, has shown the dilation to be due to blood movement alone. In the monograph which incorporates their extensive and detailed synthesis of existing knowledge of prosobranch snails, Fretter and Graham (1962) mention the work of Schiemenz, but note that in the smaller British naticid species, *Natica catena* and *N. alderi,* they could find no pedal water pores. In his excellent book on the mechanical and evolutionary aspects of body-cavities in metazoans, Clark (1964) discusses locomotion in naticids, but regards the foot in all gastropods as consisting of erectile tissue, dilated

by blood. Thus Morton (1964) in his review was perhaps justified in dismissing water uptake as a feature of naticid expansion, and in stating, "No worker has verified Schiemenz's canals. . . ."

The present work was carried out at Woods Hole at different times in the summers from 1961 to 1966. The existence of a pedal water-sinus system in the naticid, *Polinices duplicatus*, and the use of inulin-labelled sea water in its investigation, were briefly reported (Russell Hunter and Apley, 1965) in a note on temporary hyperthermia in that species. While the present results were being prepared for publication, Bernard (1968) has independently demonstrated uptake into a pedal water-sinus system in the West-Coast species, *Polinices lewisi*, though with weighing experiments involving small numbers of narcotized snails, without direct records of volumes of water involved, and without labelling experiments. The present paper reports the results of extensive weighing experiments on "trained" un-narcotized snails, including the relation of different degrees of expansion to the water volumes involved, and the construction of "balance sheet" equations involving the mass of the shell and its actual capacity. The succeeding paper (Russell-Hunter and Apley, 1968) describes and discusses the use of inulin-labelled sea water in the investigation of the relation of the various water spaces and of the rates of water exchange. A third paper is being prepared on the micro-anatomy and histology of the naticid pedal water-sinus system.

MATERIALS AND METHODS

On anatomical grounds, the family Naticidae (in the superfamily Naticacea) is placed in the suborder or order Mesogastropoda (formerly the Taenioglossa). It is worth noting that most other familiar families of predaceous gastropods using protrusible proboscides, including the Muricidae (e.g. *Urosalpinx*), Buccinidae, Nassariidae, and Conidae, differ anatomically from the naticids and are classified in the suborder or order Neogastropoda (formerly the Stenoglossa). Most work was done on the two commonest species of naticids at Cape Cod, *Polinices duplicatus* and *Lunatia heros*, collected on tidal flats at West Barnstable Harbor, at Orleans Town Pond, and at Duxbury. *P. duplicatus* survives lowered salinities and high temperatures, is the better adapted littoral species and is abundant in certain localities (Russell Hunter and Grant, 1966). *L. heros* achieves the largest size of local naticids, is less resistant, and is essentially a sublittoral species colonizing the intertidal in certain areas. A few observations have also been made on four smaller species, *P. immaculatus, L. triseriata, Natica clausa,* and *N. alderi*. All experimental snails were marked with individual numbers (using various colors of model "dopes" and nail varnishes) and specimens of *P. duplicatus* were maintained in healthy condition in laboratory aquaria for over two months.

The present experiments all depend on the fact that it proved possible to habituate individuals of the two larger naticid species to handling. After a few hours of training, a snail would remain expanded on being transferred to a dry aluminum weighing tray to be weighed in air. There was considerable individual variation in responses and in retention of responsiveness even among snails of similar size.

A triple-beam, and subsequently a torsion balance, were used for the weighings (all to the nearest 0.1 g.). An engineer's dial caliper was used to measure the shells—the measurement recorded here as "shell length" being actually the greatest

transverse diameter of the globose shell, from the outer edge of the peristome to the opposite periphery of the last whorl of the shell. The closed volumes of shells were determined by displacement weighings, each cleaned shell being filled with plaster of paris.

In the majority of weighing experiments a numbered snail, of known shell length and contracted weight, was allowed to expand. It was then transferred

TABLE I

Pedal expansion and retraction in Polinices duplicatus: weights in air, and expelled water volumes

Snail #	Shell length mm.	Contracted wt. g.	Estimated degree expansion	Expanded wt. g.	Weight difference g.	Actual water expelled ml.	Expansion Index
d1	61.0	106.2	7	261.6	155.4	136.3	246
d2	35.0	14.7	8	40.0	25.3	22.9	272
d3	40.9	24.7	5	53.8	29.1	29.2	218
d6	26.7	5.9	4	10.9	5.0	5.2	185
d7	52.2	46.0	10	170.2	124.2	111.7	370
d10	44.2	32.1	10	174.2	142.1	134.2	543
d12	36.8	16.9	10	52.8	35.9	34.3	312
d13	36.2	15.8	9	52.6	36.8	35.0	333
d16	33.2	12.0	7	29.7	17.7	17.2	248
d18	36.9	17.7	8	55.8	38.1	35.7	315
d19	33.6	12.8	8	31.7	18.9	18.6	248
d20	41.9	23.6	9	71.8	48.2	45.8	304
d22	35.9	14.4	5	27.9	13.5	13.6	194
d24	16.5	1.8	9	5.2	3.4	2.5	289
d27	49.6	45.1	5	86.3	41.2	40.6	191
d28	46.1	39.8	6	94.6	54.8	54.2	238
d31	43.5	33.7	5	58.9	25.2	25.3	175
d32	41.5	24.6	7	62.8	38.2	38.2	255
d35	44.8	35.0	6	76.8	41.8	41.6	219
d36	46.1	37.7	8	85.7	48.0	46.3	227
d41	41.2	26.6	7	69.0	42.4	41.1	259
d42	39.8	25.0	6	58.0	33.0	33.1	232
d44	52.5	49.7	9	154.3	104.6	104.5	310
d45	47.4	39.6	9	123.7	84.1	84.0	312
d46	46.9	33.4	10	142.8	109.4	109.2	428
d47	43.3	30.5	10	128.1	97.6	92.4	420
d49	46.6	33.4	8	90.4	57.0	57.5	271
d51	41.7	25.3	9	69.6	44.3	44.3	275
d201	22.8	3.9	5	7.4	3.5	3.5	190
d207	30.4	9.8	9	31.2	21.4	21.3	318
d209	48.1	35.6	9	121.9	86.3	86.3	342
d212	46.2	33.1	8	105.4	72.3	73.8	318
d213	43.6	26.9	9	79.2	52.3	52.4	294
d217	37.9	18.4	10	62.5	44.1	43.8	340
d219	41.3	24.3	10	72.5	48.2	47.6	298
d221	43.3	28.6	10	92.3	63.7	62.4	323
d223	29.0	8.6	8	24.3	15.7	15.9	283
d226	34.6	14.5	8	39.8	25.3	25.5	274
d228	41.2	22.5	10	70.7	48.2	46.7	314
d229	36.3	15.0	10	79.8	64.8	64.0	532
d232	44.3	31.9	5	66.5	34.6	34.3	208
d272	43.4	25.0	8	76.7	51.7	49.7	307

TABLE II

Repeated pedal expansion and contraction in Polinices duplicatus

Snail #	Shell length mm.	Dates measured	Contracted wt. g.	Estimated degree expansion	Expanded wt. g.	Weight difference g.	Actual water expelled ml.	Expansion Index
d4	39.8	June 28	21.5	5	39.6	18.1	19.1	184
		June 30	21.5	7	49.6	28.1	23.1	231
		June 30	21.5	8	57.2	35.7	35.6	266
		Aug. 2	20.6	8	54.0	33.4	33.3	262
d5	47.8	June 29	39.9	8	110.7	70.8	67.0	277
		July 1	39.9	6	84.9	45.0	42.8	213
		July 1	39.9	7	85.0	44.9	45.6	213
		Aug. 2	37.3	6	82.2	44.9	44.9	220
d8	47.5	July 3	35.9	10	123.8	87.9	75.9	345
		Aug. 2	34.8	9	128.3	93.5	93.6	369
d50	44.5	July 14	29.8	8	90.4	60.6	58.9	303
		Aug. 1	30.5	10	114.9	84.4	84.3	377
d210	47.5	July 8	36.8	7	101.2	64.4	63.5	275
		Aug. 20	35.0	8	107.6	72.6	71.7	307
d270	51.1	Aug. 21	40.4	9	127.9	87.5	87.2	317
		Aug. 21	40.4	5	93.2	52.8	50.9	231
		Aug. 21	40.4	7	108.0	67.6	66.0	267

to a dry weighing tray, weighed "damp-dried" in air and then forced to contract. The volume of water discharged into the tray was measured, and then the contracted snail weighed again in air. Other experiments involved different sequences.

RESULTS

Preliminary trials soon demonstrated that the weight difference between the snail expanded and contracted was nearly always equal to the volume of water expelled on contraction. This was true for differing degrees of expansion, and for both *Polinices duplicatus* and *Lunatia heros*. Individual variation was less marked in smaller snails, which tended to expand more rapidly after repeated expansions and forced contractions. Medium-sized (shell lengths 30–45 mm.) and larger (45–70 mm.) snails mostly tended to sulk after a third or fourth forced contraction. However, about a third of the medium-sized snails continued to re-expand relatively rapidly, after ten forced contractions within four hours. Such snails are responsible for a disproportionate amount of the data in this paper, and similar snails were deliberately chosen for the inulin-loading experiments (Russell-Hunter and Apley, 1968).

The main series of weighing experiments involved 91 specimens of *Polinices duplicatus* and 22 of *Lunatia heros* in 188 and 47 cycles of weighings, respectively. Table I presents results for 42 typical specimen cycles of *P. duplicatus,* and Table II shows some results of weighings repeated at intervals of up to six weeks.

It proved necessary to set up an arbitrary scale (1–10) for the degrees of expansion achieved. Only the visually estimated degrees of expansion from 4 to 10 were actually employed. Snails remaining considerably less than half-expanded were rated—4, snails half-expanded—5, two-thirds expanded—7, three-quarters expanded—9, and "considerably more than three-quarters expanded" and fully expanded—10. Ratings 6 and 8 were intermediates between the more definable 5, 7 and 9, and the subjectivity of the assessment resulted in relatively more snails being assessed in these two intermediate grades. Such estimates of degrees of expansion are shown in Tables I and II.

The last column of both tables shows a calculated expansion index, which is $M_E/M_C \times 100$ when M_E is the expanded weight and M_C the contracted weight. In Figure 1 expansion indices calculated from 188 cycles (91 specimens) for *Polinices duplicatus* are plotted against the estimates of expansion. Frequencies of index numbers are shown as histograms, at each estimated degree of expansion, and for clarity the calculated index numbers are grouped in class intervals of five units (*i.e.*, index numbers from 243 to 247 inclusive are given the class mark 245). There is fair agreement between the visual assessment and the index calculated from the ratio of weights.

Similar results were obtained with the 22 specimens of *Lunatia heros* which were habituated to handling. "Hypersensitive," and therefore untrainable, individuals were more common in this species. Specimens of *L. heros* of from 34.2 to 70.0 mm. shell length had contracted weights ranging from 13.6 g. to 133.3 g., and gave expanded weights from 24.5 g. to 319.6 g. The assessed degrees of expansion (over 47 experimental weighing cycles) mostly lay in the 5 to 7 range, and most of the corresponding calculated index numbers lay between 185 and 225, the highest index of expansion for the species being 262. It is interesting that index numbers can be calculated similarly for the 20 specimens of *Polinices lewisi* whose contracted and expanded weights are reported by Bernard (1968). These would average only 180, the highest index number achieved being about 202. The specimens of *P. lewisi* used were mostly large (mean contracted weight = 149 g.) and therefore comparable to the largest *L. heros* reported on above. Thus, to date, the most reproducible results from laboratory weighings—and the largest recorded expansion indices—have been derived from the more euryoecic, and more readily "trainable," species, *Polinices duplicatus*.

Significantly, observations on smaller naticid species were disappointing. Pedal expansion and retraction have been observed in *Polinices immaculatus*, *Lunatia triseriata* and *Natica clausa* from the Cape Cod area, and in *Natica alderi* from Scotland. In all four species, retraction is a more rapid process than in *P. duplicatus* and *L. heros*, and habituation to handling well-nigh impossible. The only one of these smaller species in which appreciable discharge of water on contraction could be detected was *L. triseriata*. Measurement was difficult: the largest specimens had shell lengths of 12.2 mm., and contracted weights of about 0.41 g. Assessment of the weight (or volume) of water involved in expansion in *L. triseriata* is hampered by proportionately large variations in the amounts carried on the surface of the snail. However, with no claims to accuracy, only about 0.25 ml. uptake is involved in large specimens of *L. triseriata*. These disappointing data may help to explain the inconclusive evidence gained from Morris's
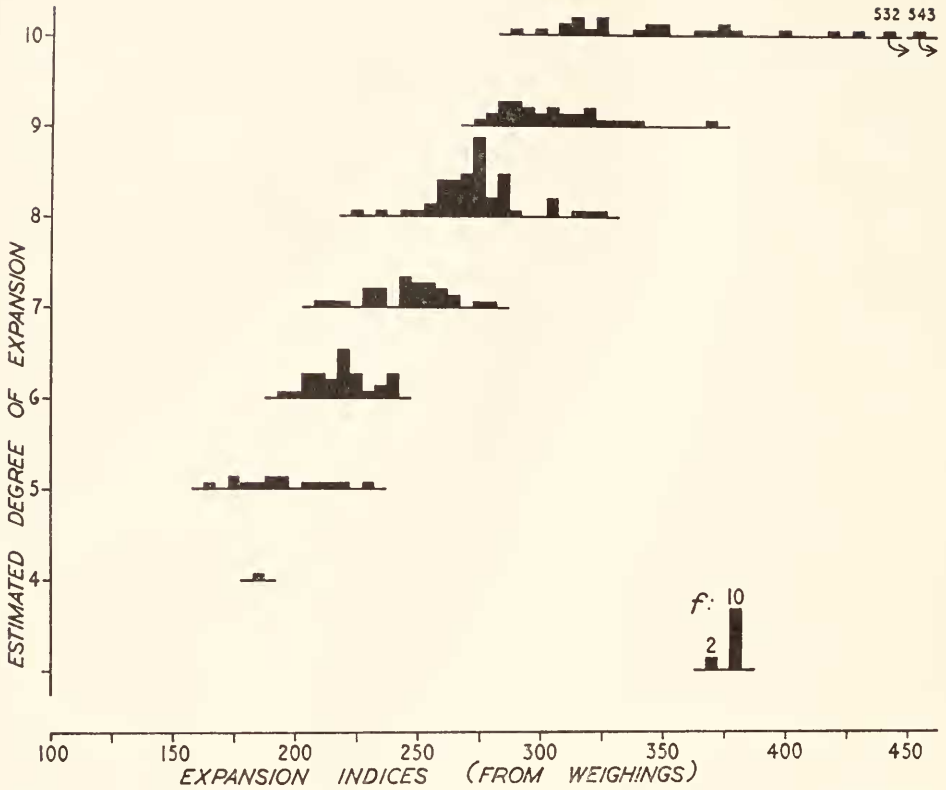
FIGURE 1. The relation of visually estimated degrees of expansion in the naticid, *Polinices duplicatus*, to the expansion indices calculated from the results of weighing contracted and expanded snails. Results derived in 188 weighing cycles from 91 individual snails are shown as histogram frequencies of index numbers. For clarity the calculated index numbers have been grouped in class intervals of five units. For further discussion see text.

(1950) study on the medium-sized Australian species, *Uber strangei*, where water uptake for most specimens must lie in the range 4–7 ml. However, results of weighing experiments on specimens of *Polinices duplicatus* as small as *Uber* were consistent and conclusive (for example, see snails d24 and d201 in Table I).

Some observations on the methods and *rates* of expansion and contraction in *Polinices duplicatus* are worth noting here. (Extensive records of the times involved in expansion were also made during the inulin-loading work—see Russell-Hunter and Apley, 1968.) Retraction can be rapid, particularly in non-habituated specimens newly brought from the field and, in such cases, can be accomplished in 2.5–4.0 seconds (medium-sized *P. duplicatus*). During such rapid contraction, the characteristic "jets" of sea water from the marginal pores of the water-sinus system along the sole edges of the mesopodium are seen. Experimentally forced contractions in "trained" snails usually take longer, and can take 10–15 seconds in medium-sized specimens that have been habituated to handling. During such slow "reluctant" contractions it is clear that almost all water (excepting that from

the mantle-cavity which is expelled through the *inhalant* siphon) is discharged *via* the mesopodium and its marginal pores; successive waves of muscular contraction pass over both the "plowshare" of the propodium, and the propodial and meta-podial folds surrounding the shell, driving the water contained in their water-sinuses into those of the mesopodial system and thence to the exterior. An account of the anatomy and histology of the system is being prepared, but a few notes on general functional morphology may be required here. Naticids retain to a great extent the three-fold division of the primitive molluscan foot. The pro-podium is large, wedge-shaped when expanded, and is the plowshare of locomotion (cutting the characteristic canal-shaped—rectangular in cross-section—tracks on the surface of sand flats). With the mesopodium, it is also the organ used for enveloping the prey and manipulating it into the correct position for the proboscis to go to work. [In *Polinices duplicatus* and *Lunatia heros*, this does not neces-sarily mean positioning the bivalve's umbones at the mid-anterior end of the pro-podium ready for boring, though this is more usual. Both species consume small and medium-sized razor-clams, *Ensis directus*, at Barnstable and elsewhere, with-out boring, by positioning the anterioventral gape of the razor-clam for proboscis action.] The posterior edge of the propodium is directed upwards in the "pro-podial shield" which envelopes the anterior third of the shell when expanded. The shield also encloses the head and mantle edge, including the inhalant pallial siphon and exhalant fold, and is responsible for molding the characteristic egg-masses or sand-collars (actually shaped between the propodial shield and the shell). The mesopodium is the largest part of the foot, provides the locomotory sole and is capable of great lateral expansion in enfolding prey and in some kinds of locomo-tion. There are no upwardly directed folds of the mesopodium. The meta-podium is archetypically the upper posterior division of the foot, last to be with-drawn in gastropod veligers after torsion, and bearing the operculum. In naticids, the metapodium when expanded conceals the operculum while its folds, shaped like a thick cup, enclose most of the posterior two-thirds of the shell. The meta-podial folds have been termed epipodial, but this term might be better restricted to upwardly directed folds of the mesopodium (which in some archeogastropods give rise to characteristic sensory structures), and it is certainly incorrect (on comparative grounds, see Fretter and Graham, 1962) to term *all* the pedal struc-tures, apart from the propodium, either "metapodium" as does Morris (1950), or "postpodium" as does Bernard (1968).

Thus the great bulk of the water discharged on retraction, and taken up more slowly during expansion, passes through the marginal pores and major water-sinuses of the mesopodium. The experiments using inulin-labelled sea water (Russell-Hunter and Apley, 1968) have shown that only about 5–7% of the volume of sea water taken up on expansion is taken in through the pallial siphon to the mantle-cavity, and only about 2% of the increased weight on expansion is due to superficial water on and between the shell and expanded surfaces. Thus about 90% of the water uptake first enters the mesopodial water-sinuses and then is pumped by contraction of the major mesopodial columnar muscle bundles into the water-sinuses of the propodium and metapodium, the marginal pores being first sealed by contraction of the smaller distal vertical muscles at the mesopodial edges. All the muscle columns are ensheathed by the lining of the

water-sinuses, consisting of a very thin pavement epithelium facing the lumina underlain by a tough layer of collagen-like connective tissue. [The water-sinuses are completely separate from the circulatory system: arterioles and branch sinuses of the hemocoel run with and through the muscle columns. Claims that blood can be involved in the fluids expelled on naticid contraction (Morris, 1950) could only be based on damaged specimens subjected to highly stressed and uncoordinated retraction. Schiemenz (1884, 1887) described the sheaths separating the water-sinuses from the tissues, and his observations are confirmed by recent work (Bernard, 1968; Russell-Hunter, in preparation).]

Normal expansion in healthy specimens of *Polinices duplicatus* takes from 3 to 8 minutes, and somewhat longer in *Lunatia heros*. Initial uptake through the minute marginal pores (about thirty on each side) depends partly on the ciliation of the epithelia around their openings but more on the "recoil" elasticity of the connective tissue sheath system. The latter forces are almost certainly augmented by the temporarily increased blood pressure *within* the muscle columns. The relative times taken in contraction and re-expansion are closely analogous to those for sea-anemones where, similarly, muscles cause contraction, and ciliary and elastic forces are responsible for expansion (Batham and Pantin, 1950). Second and successive experimental expansions within a few hours are possible in *Polinices*, but in habituated specimens the time taken in re-expansion progressively increases (mean times: for first re-expansion in a day's experiments—6.2 minutes, for fourth re-expansion within three hours—21.5 minutes).

In air, on dry surfaces, the larger naticids *cannot* re-expand. The columellar muscle can relax, which allows the operculum to gape, revealing the retracted metapodial folds and the "crumpled" mass of the mesopodium. Only when the latter is in contact with water can real expansion take place. Some experiments with medium-sized, contracted specimens of *P. duplicatus*, set up in shallow water in large weighed petri dishes, showed that expansion was possible with water depths of 3.5–4.0 mm., provided the contracted shell was placed so that the mesopodial margin came in contact with the water when the operculum gaped. Such experiments involved relatively slow expansions (13–26 minutes), and the visually estimated degrees of expansion would be 4 or 5 rather than 9 or 10, but the weight gained by each snail closely matched the water removed from the dish. Only in deeper water does full expansion occur, and only if nearly completely submerged is the mantle-cavity filled and functional. Other experimental investigations of water uptake using dyes such as phenol red were superseded by the experiments with inulin-labelled sea water reported in the next paper (Russell-Hunter and Apley, 1968).

Both in the laboratory and under field conditions, the larger naticids remain continuously expanded for many days (even weeks). The sea water expelled on the first contraction of freshly collected specimens has contained unidentified ciliate protozoans on eight occasions. From two large specimens of *Polinices duplicatus*, first discharged water samples yielded 7 and 3 living harpacticoid copepods, respectively. These were identified as *Tisbe gracilis* by Dr. Harry C. Yeatman, to whom our thanks are due. Harpacticoids have been expelled on five further occasions and have included all ages from nauplii to females with egg-sacs.

The last results to be discussed here are based on the data which were

accumulated on the actual shell weights and contained volumes for *Polinices dupli-catus*. The weight of the dry shell plus operculum (W) in 69 individuals of shell length (L) from 6.2 mm. to 60.3 mm. (mean = 27.6 mm.), ranged from 0.057 g to 38.7 g. with a mean of 7.09 g. Ratios of W/L^3 calculated for the 69 snails (W in g., L in cm.) give a mean value of 0.166. The total volume (V) of the filled shell (by displacement) in 61 individuals of shell length from 6.2 mm. to 56.8 mm. (mean = 27.3 mm.), ranged from 0.074 ml. to 58.8 ml. with a mean of 9.96 ml. Ratios of V/L^3 calculated for the 61 snails give a mean value of 0.253. These two sets of figures include smaller snails, while the habituated ex-perimental animals are all medium or large (the 48 snails of Tables I and II have shell lengths ranging from 16.5 to 61.0 mm., with a mean of 41.3 mm.).

It is perhaps worth using such volume figures to dismiss another erroneous theory of naticid expansion. This theory, discussed by Morris (1950) and Brown and Turner (1962), suggests that naticid pedal expansion could result from compensatory water being taken to spaces "around the animal, within the shell." Of course, Brown (1964) has shown that pedal expansion in the nassariid, *Bullia*, is accomplished entirely by movement of blood into foot, sea water flowing in to fill a "free space" between the visceral tissues and the shell. In an expanded *Bullia*, the volume of sea water contained within the shell, but outside the tissues, has been estimated at about twice the volume of water in the mantle-cavity, or up to 80% of the shell's volume (Brown, 1964). Nothing like this is possible in a large naticid. For example, experimental snail d209 (Table I) with a shell length of 48.1 mm. would have a calculated total shell volume of 28.2 ml. This is compatible with the recorded contracted weight of 35.6 g., and implies a (re-tracted) capacity of about 20 ml. for tissues, blood, and water. This capacity should be contrasted with the volume difference recorded (Table I) between the expanded and contracted states of 86.3 ml. Thus, application of a "free space" theory to the facts of naticid expansion is absurd.

The shell volume and weight figures can be used in "balance sheet" equations.

If T is the mass in g. of the contained tissues and retained water in the con-tracted snail, then: $T = M_C - W$.

Also, if the tissues have a s.g. near 1.0, T can be regarded as an approximately equivalent volume in ml. and, if V_S is the volume of shell material in ml., then: $T = V - V_S$.

Re-arranging these we have: $M_C = W + V - V_S$. But the s.g. of the shell is approximately 2.57 (calcite s.g. = 2.71), so that: $V_S = W/2.57$ and: $M_C = W + V - (W/2.57)$. Values assessed above of $W = 0.166L^3$ and $V = 0.253L^3$, allow us to predict the contracted weight in terms of the shell length: $M_C = 0.354L^3$. The actual contracted weights of the 91 specimens of *Polinices duplicatus* which provided the data for Figure 1 are fitted very well by this curve. Predicted values can be extended to expanded snails since the expansion index: $I = M_E/M_C \times 100$, and thus: $M_E = I \times 0.354L^3/100$ and, for example, for estimated expansions of 8 with an $I = 270$, then: $M_E = 0.956L^3$. Predicted curves based on shell length for each level of expansion can be made in this way and provide good fits for the 188 actual expanded weights on which Figure 1 is based. There is obviously an element of syllogism in such predictions of M_E, but the above predicted curve of M_C does *not* involve the actual data on contracted weights. Further, the broad

agreement of both sides in such "balance sheets" shows that no major weight factor has been omitted in this consideration of the relevance of weighing experiments to the mechanics of expansion in *Polinices*.

DISCUSSION

The historical introduction to this paper discusses how the mechanism of pedal expansion in naticid snails, correctly explained by Schiemenz (1884, 1887), was ignored or denied in the literature for eighty years. It is hoped that the present papers will provide the needed unequivocal evidence of the functioning of the pedal water-sinus system in naticids. The simple weighing experiments have already been discussed in the perspective of the differing water uptake involved in different degrees of expansion, in relation to the times involved in contraction and expansion, and in the relation to the weight and volume values for different parts of the snail. The essential equivalence of the weight loss on contraction to the sea water expelled, and the fit of actual contracted and expanded weights to values calculated in relation to shell length, are stressed. The relation of various water spaces, and the rates of water exchange are discussed elsewhere (Russell-Hunter and Apley, 1968).

There remain to be discussed certain mechanical and evolutionary aspects of the naticid water-sinus system.

The majority of movements in molluscs involve transmission of forces generated by muscle contractions through the hydraulic skeleton provided by the blood in the hemal meshwork of the molluscan hemocoel. In a large number of cases, molluscan organs are dilated and extended rather slowly by influx of blood, and are withdrawn relatively fast by intrinsic retractor muscles. The underlying anatomical pattern of obvious retractors within each structure without obvious antagonists locally placed is characteristic (Russell-Hunter, 1968). This reliance on distant antagonists, along with the unchanging total blood volume in the hemocoelic hydraulic skeleton, together are responsible for many of the peculiar features in the mechanics of molluscan locomotion and other movements. For example, limitations arise in the number of extensile structures which can be dilated and protruded at one time. If a pulmonate snail is observed in copulation, the sensory and locomotory organs of the head and foot are flaccid and crumpled, a large proportion of the blood volume being involved in dilation of the genital structures. Further, in most gastropods and bivalves the total blood volume is limited to that which can be withdrawn along with the tissues into the closed shell. To a limited extent, these difficulties can be bypassed by compartmentalization of the hemocoel. Certain mechanically efficient molluscan organs where this is the case have been investigated. Capacity to seal off a potentially variable amount of blood in an organ allows the use of intrinsic muscles in local functional antagonism. Examples include the use of radial muscles to extend the siphons (by "thinning" the siphonal walls) in tellinid clams (Chapman and Newell, 1956), and the radial arrangement of antagonists to the main propulsive circular muscles in the mantle wall of cephalopods. In both cases the fluid content of the wall can be isolated from the rest of the molluscan hemocoel and this allows the efficient use of local antagonistic muscles.

The adaptive significance of the great capacity for pedal expansion in naticids is obvious, and has already been discussed in relation to both locomotion and predation.   Mechanically it is based on the capacity for water uptake into internal spaces to provide a hydraulic skeleton of variable total volume.   Significantly the volume of the hydraulic skeleton of the pedal water-sinus system is not limited (like hemal volume) by the capacity of the closed shell.   Other molluscs, notably bivalves with fused mantle edges and massive siphons, make use of contained sea water in a hydrostatic skeleton of variable volume.   In forms like *Mya* and *Hiatella*, closure of the mantle openings allows the siphonal musculature to act as the antagonist of the shell adductor muscles around a temporarily constant volume of sea water in the closed mantle-cavity (Russell Hunter, 1949; Chapman and Newell, 1956; Russell Hunter and Grant, 1962).   This is the basis of the boring mechanism in *Hiatella* (Russell Hunter, 1949), and of the step-wise process of siphonal extension in *Mya* (Chapman and Newell, 1956).   Of course, the potential of the water-sinus system in naticids, where the total capacity of the hydraulic skeleton can be three or four times the capacity of the shell, is much greater than that of the myacean bivalve's mantle-cavity.

Compartmentalization is also important in the naticid hydraulic skeleton. During expansion, the muscular "pumping" which transfers sea water from the mesopodial water-sinuses to those of the propodium can be followed by a period of further uptake through the mesopodial pores.   During this process the already dilated and turgid propodium must be sealed off from the flaccid "absorbing" mesopodium.   Occasional inefficiencies in unhealthy or tired snails can be revealing. Normally the first stage of retraction is a rapid transfer of most of the propodal water to the mesopodium before columellar contraction.   Occasionally, the "sphincter" muscles between propodium and mesopodium remain contracted (as they are phasically during expansion) when the columellar muscle has already begun to retract the head-foot.   Rather rarely, a turgid propodium is trapped against the shell edge and injury results.   More frequently, metapodial folds are trapped between operculum and shell.   In these cases, the initial retraction is interrupted, the columellar muscle relaxes temporarily, the operculum gapes a little, the metapodium is withdrawn properly, and the retraction is completed.   Another, more frequent, inefficiency occurs during expansion when the propodium is being filled by contraction of the mesopodial muscles.   Normally, all the mesopodial pores are first sealed but, occasionally, some parts of the mesopodial margin remain relaxed and outward jets of water can be detected with dyes or suspended particles during the filling of the propodium.   Apart from the overall capacity for propodial isolation, parts of the anterior water-sinus system must themselves be operable as small "closed" hydraulic units with local sets of antagonistic muscles.   The evidence for this comes from behavioral, rather than mechanical, observations.   Part of the propodium in *Polinices duplicatus* can wrap around and pick up a small bivalve, then transfer it across or back to another temporary propodial fold, rotate the clam, and reverse it end for end.   The propodium can then manipulate it into the "correct" position for the proboscis, and form the two folds of the "vice" which holds the clam during boring.   The manipulations involved in catching an active medium-sized *Ensis* can be even more elaborate.   It should be remembered that the principal sensory organ in the functionally blind naticids is also the propodium.

(The greatly reduced eyes are "buried" behind the propodial shield in the expanded snail.)   Observations of a *Polinices* "searching" for prey with the extended propodial tip "scanning" the sand surface like an elephant's trunk, or of the capture and handling of an *Ensis*, emphasize the adaptational significance of the disproportionate pedal expansion.   There is even a report of "swimming" using undulating movements of the propodium in *P. josephinus*.   Most of the activities of the larger naticids *depend* on the mechanical properties of the pedal water-sinus system.

As with many biological problems, it is easier to discuss the adaptational significance of the pedal water-sinus system, than to speculate on its evolutionary origins.   The latter is made additionally difficult by the phyletically isolated position of the Naticidae within the taenioglossan mesogastropods.   They represent a line which has evolved the structures and habits of predaceous carnivores (like those of stenoglossans) completely independently.   The suggestion by Cox (1960) that naticids could be allied to that aberrant group of archeogastropods, the Neritacea, is not supported by the evidence of functional anatomy (Fretter and Graham, 1962) but does serve to underline the isolated position of the moon-snails.   Thus it is almost impossible to set up alleged "relatives" of naticids in which to look for simple versions or precursors of the pedal water-sinus system.   Obviously it is worth investigating the elaborate system of the larger naticids as it develops in the young snail, and it may be worth re-investigating the smaller naticids.   Some of the latter may prove to possess a simpler, and more than proportionately smaller, water-sinus system.

In spite of the paucity of evidence on evolutionary origins, two hypotheses seem worth advancing.   First, in spite of the histological nature of the sinus linings noted above, it seems most likely that the pedal water-sinus system is developed centripetally from an epidermal origin (*i.e.*, is analogous in ontology to nephridia rather than to coelomoducts).   Secondly, it seems possible that the system originated as an elaboration of the lumina of anterior or posterior pedal mucous glands like those found in certain mesogastropods, which glands are developed as epidermal invaginations.

Summary

1. In 1884, Schiemenz published an essentially correct interpretation of the mechanism of pedal expansion in naticid snails.   A historical review discusses how this was ignored or denied in the literature for eighty years, and summarizes the need for unequivocal evidence on the problem.

2. Larger naticids, including *Polinices duplicatus* and *Lunatia heros,* have an extensive pedal water-sinus system, and considerable intake of sea water is required for expansion.   On dry surfaces, in air, they cannot expand.

3. Naticids can be habituated to handling, and then weighed in air at all degrees of expansion.   Extensive weighing experiments show that the sea

water expelled on contraction is always equivalent to the weight difference between the expanded and contracted states. An index of expansion can be calculated relating expanded to contracted weight and this correlates with visual assessments of degree of expansion. Taking contracted weight as 100, half-expanded specimens of *Polinices duplicatus* have index values around 195 and fully expanded ones around 350. For example, this means that a *Polinices* weighing 46 g. contracted, takes in 124 ml. of sea water when it expands fully to a weight of 170 g. Shell weights and capacities can be incorporated in computing predicted curves which fit results from weighing live snails.

4. In healthy medium-sized specimens of *Polinices duplicatus*, retraction takes 2.5–4.0 seconds and expansion takes 3–8 minutes. Retraction is brought about by a sequence of muscle contractions; expansion is largely based on a "recoil" elasticity augmented by local hemal dilation. The larger naticids often remain continuously expanded for many days.

5. The capacity for disproportionate pedal expansion conferred by the water-sinus system is of great adaptive significance to naticid snails—particularly for locomotion in sand and for prey capture. This is discussed in relation to the hemal hydraulic skeleton and the systems of distant antagonists more usual in molluscs. The hypothesis is advanced that the pedal water-sinus system of naticids may have evolved from epidermal invaginations resembling the pedal mucous glands of other mesogastropods.

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